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On Defining Species in Terms of Sterility: Problems and Alternatives

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ABSTRACT: Despite its historic role as a criterion of species status, intersterility sensu lato is not an acceptable characteristic for delineating the genetic species or field of gene recombination. This conclusion is not new since it is in agreement with Darwin's views as expressed in *Origin of Species* (1859). The critical role of sterility in distinguishing between the prevailing genetic concept of species and its rival, the recognition concept, is demonstrated. Factors that may have led to the general acceptance of Wallace's views on speciation, rather than Darwin's, are briefly discussed.

PERHAPS BECAUSE OF ANCIENT KNOWLEDGE of the mule, people in general have long considered sterility sensu lato as the key to the delineation of species. In Western societies this belief was held first by articulate Christians and then by Christian biologists, in support of their preconceptions that were founded on the creation stories of the book of Genesis. Eventually, this belief spread by cultural osmosis to biologists in general, although they often had no commitment to the Biblical accounts of creation. Darwin attested to this situation in the opening sentence of Chapter 8 of *Origin of Species* (1859:245): "The view generally entertained by naturalists is that species, when intercrossed, have been specially endowed with the quality of sterility, in order to prevent the confusion of all organic forms." The historian Ellegard (1958:208) supported Darwin's claims with evidence from the popular and ecclesiastical journals of the 1850s. Well before this, the great geologist and committed Christian, Lyell, wrote (1832:19): "Nature has forbidden the intermixture of the descendants of distinct original stocks, or has, at least, entailed sterility on their offspring, thereby preventing their being confounded together, and pointing out that a multitude of distinct types must have been created in the beginning, and must have remained pure and uncorrupted to this day." Mayr's (1963:109) views of almost a century and a half later bear a strong generic resemblance to Lyell's: "It is the function of the isolating mechanisms [which include sterility] to prevent such a breakdown [due to hybridization] and to protect the integrity of the genetic system of species." The two authors share the view that sterility is an isolating mechanism. Lyell saw the function of sterility as the protection of a species' divine, and Mayr its genetic, integrity.

While A. R. Wallace and T. H. Huxley both subscribed to this view, Darwin's ideas were strikingly heterodox. The opening to Chapter 8 of *Origin of Species* (1859:245) continues: "This view certainly seems at first probable, for species within the same country could hardly have kept distinct had they been capable of crossing freely. The importance of the fact that hybrids are very generally sterile, has, I think, been much underrated by some late writers. On the theory of natural selection the case is especially important, inasmuch as the sterility of hybrids could not possibly be of any advantage to them, and therefore could not have been acquired by the continued preservation of successive profitable degrees of sterility. I hope, however, to be able to show that sterility is not a specially acquired or endowed quality, but is incidental to other acquired differences." There is no hint here of a function for sterility as an isolating mechanism.

When we define adaptation strictly (Wil-

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liams 1966), Lyell's and Mayr's statements clearly show that these authors have regarded sterility as an adaptation, while Darwin considered it to be an incidental effect of adaptive change.

One of the problems facing anyone attempting to understand Mayr in depth is that he is inconsistent, as was Dobzhansky, and as are many other evolutionists. It is quite possible to find that he has also espoused Darwin's viewpoint that sterility is an "effect" not an "adaptation" (mechanism) (e.g., Mayr 1963:551), and that sterility cannot be used to delineate species (Mayr 1942: 119). Elsewhere, however, Mayr advocates "instantaneous speciation," which entails a definition of species in terms of sterility and a belief that a new species can arise as one individual (Mayr 1970:254). I have therefore been obliged to emphasize the view most consistent with his species definitions and his statements on the ad hoc nature of isolating mechanisms; these are worded quite unambiguously in many places, for example, in Mayr (1963:20, 91, 109, 129, 548). I appreciate that I am attempting a difficult task because I am certain to be accused of distorting the author's views, but this is a hazard in attempting to understand an author's viewpoint when his writings are extensive and inconsistent. It should be made clear that it is the detection of inconsistencies with the current paradigm that has driven me to put forward an alternative view of species that is less inconsistent and yet in keeping with the critical data from observation and experiment (see Paterson 1985 for more details).

The object of this paper is to reexamine sterility as a basis for defining species. This can be done rationally only within the constraints of a particular genetic concept of species, for sterility is seen differently under different genetic concepts of species.

SPECIES IN GENETIC TERMS

Carson (1957) pointed out that species are fields for gene recombination, and I think that few would contest this point. Disagreement exists over how the field for gene recombination is delineated. Two alternative suggestions have been made. One is the isolation concept: The field is determined by a diverse set of characters, the isolating mechanisms, the function of which is to preserve the integrity of the genetic system of the species (Mayr 1963:109, 1982:272). The other is the recognition concept: The characters of a species that function to bring about fertilization in a population's normal habitat automatically delimit the field for gene recombination. Earlier writers have consistently failed to notice that these ways of looking at species are conceptually quite distinct. This results in conflation occurring more commonly than even Verne Grant noticed (Grant 1971:35). Thus, the isolation concept is the heart of the biological species concept of Dobzhansky and Mayr, freed from conflation with the recognition concept.

The isolation concept is a relational concept, one species being defined in relation to another. This was seen by Mayr (1963:20) as an advantage: "Species are more unequivocally defined by their relation to nonconspecific populations ('isolation') than by the relation of conspecific individuals to each other. The decisive criterion is not the fertility of individuals but the reproductive isolation of populations." This emphasis (which distinguishes the isolation concept from the recognition concept) is crucial to the consideration of sterility as a basis for delineating species.

STERILITY AND THE ISOLATION CONCEPT

It has long been known that sterility s. lat. is an unsatisfactory criterion for delineating the limits of a field for gene recombination (Darwin 1859:245ff, Mayr 1942:119). I shall therefore restrict discussion to aspects of the matter that are critical for the isolation concept.

Mayr (1970:12) wrote: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." It is fundamental to the assessment of the isolation concept of species to understand the nature and origin of the iso-

lating mechanisms on which the reproductive isolation (i.e., delineation of the field for gene recombination) depends. The term "mechanisms" implies that they are adaptations (Crowson 1970:221, Futuyma 1979:408, Williams 1966:9). This in turn implies that they have been "fashioned by selection for the goal" of "protecting" the "genetic integrity" of a species. It is my view that this inappropriate use of the term "mechanism" has been a serious disadvantage to evolutionary theory through the loss of clarity of thought.

The generally recognized isolating mechanisms have been classified by Mecham (1961) as either pre- or postmating mechanisms (Mayr 1963:92). This at once demonstrates their fundamental heterogeneity, because postmating mechanisms cannot originate under selection, while premating mechanisms conceivably can. For this reason alone it is inconsistent to call sterility s. lat. an isolating mechanism. Since sterility is an unsatisfactory basis for delineating species (Mayr 1942:119), and since postmating "mechanisms" are fundamentally different from premating mechanisms, they are obviously out of place in a table of isolating mechanisms. How can we discuss intelligently the nature and origin of isolating mechanisms if we include totally extraneous elements among them (Mayr 1963:91)?

These objections to sterility as sufficient grounds for delimiting a field for gene recombination have important consequences. When a tetraploid angiosperm arises within the range of a diploid species, this is unequivocally "instantaneous speciation" according to Mayr (1970:254). This opinion has long been a source of disagreement between geneticists and plant taxonomists who, not surprisingly, are reluctant to name as distinct species-taxa organisms that may be indistinguishable structurally from their diploid relatives (Cronquist 1978). Mayr and others who accept the isolation concept regard the tetraploid (individual, not population!) as being reproductively isolated from the parental diploid individuals, because the offspring of any cross between the two will yield triploid progeny that are more or less sterile due to meiotic difficulties. [In fact, in population genetics terms, s is seldom unity (Lewis 1967).]

This is actually not a satisfactory scenario as it stands; it requires a good deal of propping up before it begins to look like a speciation model. If the polyploid and diploid plants are committed to outbreeding, the newly arisen tetraploid will simply be eliminated (Li 1955, Paterson 1981). Subsidiary propping up is needed. Usually, this is in the form of the tetraploid persisting through alternative reproductive strategies (e.g., by vegetative reproduction or self-fertilization). But, of course, uniparental organisms are not covered by any of the genetic concepts of species. In a biparental species, the newly arisen tetraploid will be eliminated, as has already been emphasized. Furthermore, Lewis (1967) has pointed out that gene exchange is not completely interrupted between tetraploid and diploid individuals. Finally, what does gene exchange in such a case mean? The "gene pool" of the tetraploid is a subset of the gene pool of the diploid population. The only consequence that could result from total reproductive isolation of the two populations is that they could eventually evolve independently. This, however, would be more or less prevented by even quite a low gene flow between them.

It might be argued: But in nature one observes genera within which the species differ in their levels of ploidy; clearly polyploidy has been the major cause of speciation here. How clearly is this established? Such arrays of congeneric species do not establish that polyploidy led directly to their origination as species. With this in mind, consider the following points: How do we know that the congeneric species of the array did not arise under the conditions of allopatric speciation as other species do? Perhaps the only role that polyploidy has (regardless of whether we are considering allopolyploidy or autopolyploidy) is that it makes sympatry between diploids and polyploids impossible. Polyploid seeds dispersed into different allopatric habitats, to which they may well be more suited, could then speciate by adapting to the new conditions in the usual way. The

usual argument involves the old fallacy of inferring causality from a correlation. It is the same fallacy that led White (1978) and others to infer causality for speciation from observing that two congeneric species differ by a fixed gene rearrangement. As Carson et al. (1967) and others have observed, such correlations with speciation are adequately explained by understanding that speciation involves small populations, which, in turn, favor the fixation of such rearrangements.

These few points are sufficient to call seriously into question the conventional views on speciation via polyploidy, as well as Mayr's views on sterility as a "fully efficient" isolating mechanism that would enable two populations (diverged in allopatry) to return to sympatry where "reinforcement" could occur (Mayr 1963:551).

Sterility occurs among plants for other reasons than from polyploidy. A much cited example should perhaps receive further consideration: *Clarkia biloba*/*C. lingulata* (Lewis 1953, Lewis and Raven 1958). In this case, *C. lingulata* evidently arose through extensive chromosome repatterning in a small isolated population (Lewis 1966). Translocation experiments (Lewis 1961) provided support for the view outlined above that sterility is not an efficient primary isolating mechanism, and supported the prediction from population genetics theory that the rarer population will generally soon be eliminated. Lewis (1961) provided evidence that pollinators do not distinguish between *C. lingulata* and its parental form. At present, there appear to be two small isolated populations of *C. lingulata* surviving in allopatry in much the way that was suggested for polyploids while they speciate allopatrically. Thus, in this view, neither the occurrence of polyploidy nor chromosomal repatterning as bases for cross-sterility constitute rapid speciation, but merely a factor possibly leading to speciation in allopatry. This topic will be considered further in the next section.

Darwin (1859) drew attention to the fact that interfertility often exists between undoubted species. Since then, many other examples have become known (Mayr 1963:90). A widely quoted example (Mayr 1963:90) is that of the interfertility of the common sympatric duck species, the Mallard (*Anas platyrhynchos*) and the Pintail (*A. acuta*), two species which are not even very closely related. Darwin was fully aware of this case, and provided many other examples (Stauffer 1975). Darwin (1859:250) also drew attention to the fact that sometimes intraspecific crosses are less fertile than some interspecific crosses involving the same species. It is conventional to talk of the sterility of crosses involving flowers on the same plant as *incompatibility*, but one should be conscious of the fact that to do so may be to mislead, since in some cases at least, no new phenomenon is involved (Heslop-Harrison et al. 1974). Accordingly, the practice should perhaps be reviewed since it could allow us to persist with our preconceptions. It is not easy to see how a self-incompatibility system could be selected to function as an outbreeding device, for self-incompatibility is obviously generally more disadvantageous than the possible disadvantages of inbreeding depression. On the other hand, selection for outbreeding devices such as distyly is conceivable as a device to counter preexisting, fortuitously disadvantageous "self-incompatibility."

As has already been made clear, it is also impossible to evolve a system of interspecific incompatibility through natural selection. One wonders why more attention has not been paid to these points by workers on pollination mechanisms, since they would provide a new perspective to their work.

Sterility has a special importance under the isolation concept, because it can obviously be acquired in allopatry, and is thus compatible with allopatric speciation. It can provide the basis for selection for true "isolating mechanisms" should diverged populations return to sympatry (Mayr 1963:551). Although Mayr has always strongly supported allopatric speciation, he was aware that it posed problems to anyone who believed in speciation as an adaptive process: "They [isolating mechanisms] are ad hoc mechanisms. It is therefore somewhat difficult to comprehend how isolating mechanisms can evolve in isolated populations" (Mayr 1963:548). However, it is curious that

he should have ignored the fact that reinforcement is really not to be expected when two diverged populations with hybrids of reduced fitness meet; what would be expected under these conditions is that natural selection would act to eliminate the cause of sterility, or the less common population if sterility is absolute (i.e., $s = 1$) (Lambert et al. 1984, Paterson 1978). If an author were to adopt an extreme position and advocate that all "isolating mechanisms" evolve in isolation by pleiotropy, they could not then be called "mechanisms" as they are obviously effects. It is then not possible to believe that speciation is an adaptive process as did Mayr (1949:284) and Dobzhansky (1976:104), and "isolating mechanisms" can no longer be treated as ad hoc characters. Perhaps enough has been said to support and extend the early view of Mayr (1942) that sterility is not in itself satisfactory as the basis for defining species, even when reproductive isolation is the criterion for species, regardless of whether authors list it or its variants as "isolating mechanisms."

STERILITY AND THE RECOGNITION CONCEPT

Sterility under the recognition concept of species takes on a different aspect entirely. Paterson (1982*a*, 1985) has defined as a species the most inclusive population of individual biparental organisms that share a common fertilization system. The fertilization system of a species comprises all characters that contribute to the achievement of fertilization. These characters are diverse and include such characters in the mating partners as the design features of the gametes, those determining synchrony in the achievement of reproductive condition, the coadapted signals and receivers of mating partners, and their coadapted organs of gamete delivery and reception.

The adaptations of the fertilization system act efficiently under the conditions of the normal habitat and way of life of the organisms. (Way-of-life characters are those such as nocturnal versus diurnal activity cycles, sessility versus motility, etc.) The fertilization system leads to positive assortative mating among members of a population in its normal habitat. This is the same as saying that the fertilization system determines the limits of the field for gene recombination in nature, and it does so without any reference to any other field for gene recombination. The recognition concept is not a relational concept (Paterson 1985). Thus, speciation in geographic isolation poses for it none of the conceptual problems that it does for the isolation concept. The consequence of all this is that species are incidental results of adaptational and stochastic change in isolated small populations. Adaptation of the fertilization system to the new conditions occurs just the same way as do all other adaptive characters; no special reliance on pleiotropy is involved.

Applying this concept to the study of sterility s. lat. leads to quite different insights from the isolation concept. Let us examine the case of *Clarkia biloba* and *C. lingulata* in this light. Lewis (1961) states explicitly that pollinators do not distinguish between these two populations when they are brought into sympatry by geneticists, and that crosses between them are intersterile, although the *C. lingulata* gene pool is probably a mere subset of that of *C. biloba*. The sterility is due to problems with meiosis caused by the complex chromosomal rearrangements that distinguish the two populations. As far as these data go, they indicate quite clearly that the two populations share a common fertilization system and are conspecific. According to the predictions of population genetics algebra (Li 1955), such populations should not be able to coexist, and the least abundant population should be eliminated rather quickly. Transplantation studies by Lewis (1961) support this expectation, with three out of the four populations conforming within the five generations spanned by the study. Harper and Lambert (1983) have carried out a uniquely planned and careful experimental study of such situations, which are also in agreement with Lewis' observations. Computer simulations point the same way (Lambert et al. 1984).

To summarize this part: Obviously, sterility cannot be among the adaptations to

bring about effective fertilization (the fertilization mechanisms); it is clearly not a relevant factor in delineating the field for gene recombination of a species. Thus, the diverse forms of intersterility [including those due to autopolyploidy, self-incompatibility in monoecious plants, and "cytoplasmic incompatibility" (Laven 1967) as found in *Drosophila paulistorum* and the *Culex pipiens* complex] are regarded as intraspecific phenomena. This conclusion is in sharp contrast to interpretations based on the isolation concept, and is an answer to those who believe the two concepts to be "opposite sides of the same coin."

DISCUSSION

Sterility s. lat. is of central significance for evolutionary theory because of the ancient association of sterility with interspecific crossing exemplified by the mule. Sterility was thus first conceived as an "isolating mechanism," filling a role required by two separate and independent commitments of Western society: The first, a commitment to purity of lineage required by the practices of ancient animal and plant breeders; and the second, a commitment to the creation stories of Christianity and Judaism, which required the preservation of the Creator's handiwork. With this existing, subliminal, cultural bias, it is scarcely surprising that Wallace's views on the nature of species were preferred to Darwin's (Paterson 1982*b*). We are told (Mayr 1963) that Darwin eliminated the species as a concrete natural unit, and thereby neatly eliminated the need for a solution to the problem of how species multiply. In fact, Darwin conceived species much as many taxonomists and others, in practice, do today. Furthermore, he did discuss the origin of species under natural selection (Darwin 1859:104–105). What Darwin saw—and Wallace did not see—was that species are not adaptive devices, but incidental products of adaptive evolution. In this he differed not only from nearly all his philosophical predecessors, but also from A. R. Wallace, J. T. Gulick, G. C. Robson, R. A. Fisher, Th. Dobzhansky, and Ernst Mayr (Paterson 1982*b*). This unique contribution of Darwin's is probably his most revolutionary, and is the one that has scarcely been noticed except by philosophers (Hull 1973:56, Kuhn 1970:172).

Sterility focuses our attention sharply on the importance of adhering to a concept of species that is logically consistent. It is not a matter of fashion or convenience, but a vital matter of basic comprehension. As Darwin said 126 years ago: "The case is especially important," not only for the theory of natural selection, but for understanding the genetic nature of species.

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